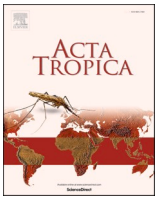
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Environmental predictors of filarial infection in Amazonian primates Ecological factors and primate filarial infection

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A B S T R A C T

Filarial nematode infections are common in primates, but have received little attention in the Neotropics. Epidemiological data on filarial infections in primates are still too sparse to fully understand the complex of this parasitism, especially because of the difficulty in studying the ecology and epidemiology of wild primates.. We describe natural infections by *Dipetalonema* parasitizing 211 primates belonging to eight free-living primate genera in Amazonia, and assess the relationships between parasitic indicators and climatic (rainfall and river level), ecological (fruiting periods of plants) and biological (sex, species' body mass, group size and density) factors. The overall prevalence was 64.4% (95% CI: 64.0 – 64.9); parasitic mean abundance (N filariae per individual) and parasitic mean intensity (N filariae per infected host) of infection were 11.9 (95% CI: 8.3 – 15.6) and 18.4 (95% CI: 13.4 – 23.4) filariae/individual, respectively. Although we observed differences in parasitic parameters among primate genera, there was no correlation between parasitic parameters with density, body mass or group size. *Sapajus, Cebus* and *Lagothrix* had the highest prevalence and parasitic mean intensity. Using *Lagothrix lagotricha poeppigii*, the most sampled species ($n = 92$), as a model, we found that the number of filariae per infected host was associated with fruit production in swamp forests during the dry season, the time of food scarcity. The long periods of food shortage may cause environmental stress on primates, impairing their immune defenses and leading to increased parasite load but not affecting infection prevalence. However, the lack of information on vector ecology, key to understand risk factors associated to infection rate, prevents confirming the existence of an infection pattern dependent on food availability.

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1. Introduction

Human filariasis, particularly that caused by *Mansonella ozzardi* (Beltrán et al., 2008), is a frequent but neglected disease in Amazonia (Medeiros et al., 2009; Herrera et al., 2013). Clinical manifestation in human filariasis depends on the filarial species and infected organ, but frequently includes skin and ophthalmic lesions, joint pain, headache, and lymphadenopathy (Branco et al., 1998; Adami and Herzos, 2008). Filarial nematode infections from the genera *Dipetalonema* and *Mansonella* (*Tetrapetalonema*) have long been detected in wild non-human primates (NHP) in Neotropical forests (Eberhard et al., 1984; Bain et al., 1986), and recently, high prevalence of filariasis has been recorded in free-living NHPs in the northeastern Peruvian Amazon (Conga et al., 2018a, 2018b) and in northeastern Argentina (Vanderhoeven et al., 2017).

Epidemiological data on filariasis in both humans and wild NHP are scarce, largely because of the difficulty in obtaining biological and epidemiological samples. Thus, integrative ecological studies on parasites, hosts and their habitats are required to understand the dynamics of human infections. Filariasis infection depends on the presence of vectors; hematophagous arthropods from the Ceratopogonidae and Simuliidae families, whose populations are in turn determined by seasonal climatic factors, such as rainfall and river level (Medeiros and Py-Daniel, 2004). In addition, the reproductive status and the food availability, often driven by climatic seasonality, may also influence the intensity of parasitic infection due to hormonal changes and the nutritional status of hosts (Klein, 2004).

In this study, we determined parasitic indicators of filariasis in eight NHP genera from the Peruvian Amazon, and described the relationship between infection rates and ecological (percentage of trees bearing fruits), biological (density, group size and body mass) and climatic factors (rainfall and river water level).

2. Material and methods

2.1. Study area

The study area covers three geographic sites in the Loreto region, northeast of the Peruvian Amazon, in the Yavari-Mirin, Corrientes and Pastaza River Basins. These areas are inhabited by remote rural communities relying on agriculture, fisheries and subsistence hunting. The climate in the region is typically equatorial with annual temperatures varying between 22 °C to 36 °C, relative humidity of 80% and annual rainfall between 1500 and 3000 mm^3.

2.2. Collected samples and obtaining of filariae specimens

We sampled primate specimens between 2009 and 2015 as part of a participatory conservation program that involves local subsistence hunters in implementing community wildlife management in the communities of Corrientes (José Olaya, Jerusalén), Pastaza (Andoas, Andoas Viejo, Titiyacu, Los Jardines) and the Yavari-Mirin River Basin (Nueva Esperanza). Local hunters were trained to record the date, species, and gender of all animals of all taxa hunted during their normal subsistence activities. Hunters were also trained to handle hunted animals hygienically and to remove the entire abdominal and thoracic organs from specimens and to store them in a 4% formaldehyde fixative solution. The procedure was performed for various groups of mammals and birds, not only for wild NHP, avoiding inducing NHP hunting. Hence, no additional mortality for the purpose of this study was caused. Adult filariae located in the abdominal and thoracic cavities and adhered to the external surface of the organs were removed, washed in saline solution, preserved in 70% ethanol, and identified using the taxonomic keys available in Bain et al. (1986) and Bain et al. (1987).

2.3. Parasitic indicators

For the calculation of parasitic parameters, we considered the *Dipetalonema* genus, which was observed in all infected NHPs. Parasitic indicators for each host species, and for all primates pooled were calculated according to Bush et al. (1998). Indicators were: prevalence (percentage of hosts with filariae), parasitic mean abundance (PMA, number of parasites divided by the number of infected and uninfected hosts, expressed as number of filariae per host), parasitic mean intensity (PMI, number of parasites divided by the number of infected hosts, expressed as number of filariae per infected host), and amplitude range (AR, minimum and maximum number of parasites in a sample).

2.4. Biological variables of hosts

Biological variables included the sex and female reproductive state (pregnant/non-pregnant) of each primate specimen, and the average body mass, average group size, and density of each species (Table 1). The sex and female reproductive state were determined through examinations of the genitalia in each hunted specimen. We considered females with at least one embryo or fetus to be pregnant, and females without embryo or fetus as non-pregnant. Since we could not obtain the body mass of each individual, we used the average body mass for each NHP species obtained from the available literature (Emmons and Feer, 1990; Hershkovitz, 1990; Ford, 1994; Smith and Jungers, 1997; Lu, 1999; Jack, 2007).

We estimated the density (individuals/km^2) and the average group size (individuals/group) of each NHP species only in the Yavari-Mirin River from direct sightings conducted on twelve 4-km wide transects monitored from 2008 to 2012, with a total of 1173.5 km survey effort in upland and flooded forests. Transects were opened prior to the surveys and researchers and local residents walked each one multiple times. Two observers (a technician and a local resident, or two local residents) walked the trails between 6:00 h and 15:00 h at an average speed of 1.5 km/h. When a group of NHP was encountered, the number of individuals was recorded, and the perpendicular distance from the trail to the first individual sighted was measured with a measuring tape. We sighted 1336 groups of the NHP, totaling 10,543 individuals. Distance 7.1 software was used to estimate population density (number of individuals/km^2) of each NHPs species (Peres, 1999; Buckland et al., 2001).

2.5. Climatic and plant phenological variables

Climatic and plant phenological variables were only collected in the study area of the Yavari-Mirin River basin. Information on river water level (in meters above sea level, m.a.s.l.) and rainfall (in mm^3) in each month-year was obtained from the Yavari River hydrological station, about 50 km from the study area and monitored by National Water Agency of Brazil (HidroWeb, *Estirão do Repouso* Station, http://www.snirh.gov.br/hidroweb/).

To determine annual changes in ripe fruit availability in the Yavari-Mirin River basin, three transects were established from random starting points in upland forests and palm-dominated swamps, which were sampled for one year (2004). All sections were 5 m wide, except one in upland forest, which was 20 m wide (Pitman et al., 2003). We marked and identified all trees with diameter at breast height (DBH) >10 cm as well as all lianas with DBH > 7 cm (following Ayres, 1986). Plants were sampled until the rate of new species discovery decreased (Sutherland, 2000), determining the length and area of transects in each forest type. Five hundred and eighty-nine trees and lianas were sampled in 8970 m^2 of dryland forests and 386 trees and lianas in 5150 m^2 in palm swamps. In the middle of each month, we observed the canopy of each marked tree and liana with binoculars, recording the presence or absence of ripe fruits in each individual sampled.

Table 1
Parasitic mean intensity (PMI, N filarid by infected host), amplitude range (AR, N minimum and maximum filarid per infected host and median of PMI), parasitic mean abundance (PMA, N of filarid by host) and prevalence (%) of infection by three species of filariae in free-living non-human primates ($n = 211$) in all study areas, the Yavari-Mirin, Corrientes and Pastaza River Basins. Different letters within columns indicate significant differences at $P \leq 0.05$.

Species	Prevalence (%)				PMI	AR (median)	PMA
	D. gracile	*D. caudispina*	*D. freitasi*	Total%			
Saimiri spp.	100 (04/04)	0 (0/04)	0 (0/04)	100 (04/04)^{abc}	27 ± 23.2^{ab}	9–60 (19.5)	27.0 ± 23.2
Ateles spp.	75 (03/04)	75 (03/04)	0 (0/04)	100 (04/04)^{abc}	11.5 ± 11.8^{ab}	4–29 (7.0)	11.5 ± 11.8
Cebus spp.	90 (09/10)	30 (03/10)	0 (0/10)	90 (09/10)^{ab}	28.9 ± 39.9^{a}	1–124 (12.0)	26.0 ± 38.7
Lagothrix spp.	73 (76/104)	1 (01/104)	0 (0/104)	74 (77/104)^{a}	21.6 ± 21.3^{a}	1–108 (16.0)	15.9 ± 20.6
Sapajus spp.	65 (32/49)	14 (07/49)	0 (0/49)	65 (32/49)^{ab}	10.9 ± 13.4^{ab}	1–61 (6.5)	7.1 ± 12.3
Cacajao spp.	0 (0/12)	0 (0/12)	50 (06/12)	50 (06/12)^{ab}	9 ± 10.6^{ab}	1–24 (3.5)	4.5 ± 8.5
Alouatta spp.	20 (02/10)	0 (0/10)	0 (0/10)	20 (02/10)^{b}	9 ± 5.7^{ab}	5–13 (9.0)	1.8 ± 4.2
Pithecia spp.	11 (02/18)	0 (0/18)	0 (0/18)	11.1 (02/18)^{c}	3.5 ± 2.1^{b}	2–5 (3.5)	0.39 ± 1.2
Total	61 (128/211)	7 (14/211)	3 (06/211)	64.4 (136/211)	18.4	1–124 (12.0)	11.9

2.6. Statistical analysis

We used generalized linear models (GLM) and Classification and Regression Tree models (CART) to evaluate the influence of biological and environmental variables on parasitic indicators: parasitic prevalence (binomial distribution) and PMI (number of filariae per infected host, Poisson distribution). Depending on the availability of sufficient sample size, and the sources of the ecological, phenological and climatic information two statistical designs (biological and environmental) were conducted for both parasitic prevalence and intensity of infection.

Firstly, in the biological statistical design we tested the biological variables (host genera, sex, body mass, group size, population density and study area), for all primates sampled in the Pastaza, Corrientes and Yavari-Mirin River basins. Secondly, in the environmental statistical design, we evaluated the environmental variables (monthly rainfall, monthly number of rainy days, monthly river water level, and percentage of trees bearing fruits both in upland and swamp forests) using *Lagothrix lagothrica poeppigii* in the Yavari-Mirin River basin as our model species, due to higher number of samples ($n = 92$).

In the GLM's analyses (R package stats, version 3.6.2), we first tested the best family of distribution for the analyses, comparing these based on QQ-plots of the residuals, and on the Akaike Information Criteria (AIC). Secondly, we tested for collinearity using the variance inflation factor (VIF, Marquardt, 1970), which measures how strongly each predictor can be explained by the rest of predictors. A VIF = 5 was set as a threshold to remove any variable from the model as signal of collinearity problems. We calculated VIF for all predictors and monthly rainfall (VIF: 5.499), was excluded from the environmental statistical design. Then, to select the best combination of predictor variables, we built a model where all the predictor variables were included and used the stepwise function (R package stats, version 3.6.2). The final model, in terms of retention of predictor variables, was defined based on AIC values (Burnham and Anderson, 2004), in which the model with the lowest AIC was selected. The final model was also executed as a CART model (R package rpart, version 4.1–15, Therneau et al., 2013).

Descriptive statistics were expressed as mean ± standard deviation (SD). All statistical analyses were performed using the software R 4.0.5 (R Core Team, 2021), and statistics with a probability value of 0.05 or lower ($P \leq 0.05$) were considered significant.

3. Results

During the study period, 211 NHPs were sampled, including 104 wooly monkeys *Lagothrix* spp. (L. *l. poeppigii*), 49 large-headed capuchins *Sapajus* spp. (*S. macrocephalus*), 18 monk saki monkeys *Pithecia* spp. (*P. monachus and P. aequatorialis*), 12 red uakari monkeys *Cacajao* spp. (*Cacajao calvus ucayalii*), 10 red howler monkeys *Alouatta* spp. (*A. seniculus*), 10 white-fronted capuchins *Cebus* spp. (*C. unicolor* and *C. yuracus)*, four squirrel monkeys *Saimiri* spp. (*S. macrodon*) and four spider monkeys *Ateles* spp. (*A. chamek* and *A. belzebuth*). Of all NHP sampled, 114 (57.3%) were male and 85 (42.7%) were female (70 non-pregnant and 15 pregnant females). In 12 individuals the genital organs were not collected and therefore we do not have sex information. From these hosts, 2502 adult filariae belonging to three species were obtained, parasitizing the abdominal and thoracic cavities: *Dipetalonema gracile* (Rudolphi, 1809), *Dipetalonema caudispina* (Molin, 1858) and *Dipetalonema freitasi* (Bain et al., 1987).

Firstly, we compared parasitic prevalence and intensity between genera, sexes, female reproductive status and study area for all NHP hosts evaluated in the Pastaza, Corrientes and Yavari-Mirin River basins. The total prevalence of filariasis of *Dipetalonema* spp. was 64.5% (136/211) (95% CI: 64.0 – 64.9) in all NHPs examined. Table 2 shows all parasitic indicators for the 211 NHP evaluated in the eight host genera evaluated in the three study areas. Of all sampled specimens, 35.5% (75/211) were non-infected, 29.9% (63/211) were lightly infected (1–10 filariae per host), 31.3% (66/211) moderately infected (11–60 filariae per host), and 3.3% (7/211) were heavily infected (>60 filariae per host).

We found a prevalence of 66.1% (125/189) for the Yavari-Mirin River basin, 57.1% (4/7) for the Corrientes River basin, and 46.7% (7/15) for the Pastaza River basin; and PMI was 11.4 ± 19.6, 9.5 ± 7.0, and 51.0 ± 23.1 filariae per host, respectively. Prevalence was 64.0% (73/114) for males and 69.4% (59/85) for females, and PMI was 17.8 ± 21.4 specimens per host for males and 19.5 ± 21.6 for females. Pregnant females had a prevalence of 75.0% (9/12), PMI of 15.8 ± 18.3, and PMA of 11.8 ± 17.2 specimens per pregnant female; while in non-pregnant females, prevalence was 68.5% (50/73), with PMI of 20.2 ± 22.2, and PMA of 13.8 ± 20.6 specimens per female.

Saimiri, Ateles and *Cebus* showed the highest prevalence (100%, 100% and 90%, respectively), while *Cebus, Saimiri* and *Lagothrix* presented the highest mean PMI (28.9, 27.0 and 21.6 filariae per infected host, respectively) and PMA (26.0, 27.0 and 15.9 filariae per total host analyzed, respectively). In the biological statistical design, significant differences were observed in the parasitic prevalence (GLM, AIC = 218.9) among the host genera (P = 4.215e-07). Based on parasitic

Table 2
Body mass (in kg), group size (in individuals/group), density (in individuals /km^2) of the eight free-living non-human primate species (n = 189) in the Yavari-Mirin River Basin.

	Body mass (kg)	Group size (ind/group)	Density (ind/km^2)
Alouatta seniculus	6.1	4.08	1.27
Ateles chamek	8.8	4.51	3.45
Cacajao calvus	3.2	26.47	5.57
Cebus albifrons	2.9	5.96	4.04
Lagothrix l. poeppiggii	7.1	9.72	45.81
Pithecia monachus	2.4	3.4	9.12
Saimiri macrodon	0.7	15.21	22.54
Sapajus macrocephalus	3	5.673	9.19

prevalence, the CART model (R^2 = 28.57%) classified the host genera into two clusters, with lower prevalence (14.28% of being positive) in *Alouatta* and *Pithecia*; and higher prevalence in *Ateles, Cacajao, Cebus, Lagothrix, Saimiri* and *Sapajus* (73.59% of being positive). Significant differences were also observed in PMI (GLM, AIC = 2515.32) among the NHP genera (P < 2e-16), and the study area (P < 2e-16). The host genera were firstly selected in the CART model (R^2 = 16.95%, Fig. 1A) and divided into two clusters based on PMI; *Alouatta, Ateles, Cacajao, Pithecia* and *Sapajus* had on average 1.87 filariae per infected host, and *Cebus, Lagothrix* and *Saimiri* had 2.70 filariae per infected host. The CART model also found differences within *Cebus, Lagothrix* and *Saimiri* hosts in relation to the study area; primates from the Pastaza River had more filariae in comparison with those from Corrientes and Yavari-Mirin (3.46 *versus* 2.64 average number of filariae per infected host, respectively). Sex, body mass, group size and population density had no significant effect on the parasitic indicators.

In the environmental statistical design, no significant difference was observed in the parasitic prevalence (GLM, AIC = 94.79). However, significant differences were found in PMI (GLM, AIC = 1154.28) related to the percentage of trees bearing fruits in swamps forests (Estimate = −0.0871, P < 1.19e-09) and monthly river water level (Estimate = −0.2575, P = 0.00238). The GLM results showed that each 1% increase of trees bearing fruits in swamps forests and 1 m increase in monthly river water level reduced the number of filariae per infected host by a factor of 0.916 (8.3%) and 0.773 (23%), respectively. The CART model with higher proportion of the variance explained (R^2 = 20.77%, Fig. 1B) selected the percentage of trees bearing fruits in swamps forests as the most important variable, with the value 0.5% as threshold dividing the PMI into two clusters (< 0.5% with 41 filariae per infected host, covering the months of September and October, Fig. 2). When the percentage of trees bearing fruits in swamps forests is > 0.5%, the monthly river water level divides the PMI in three clusters (monthly river water ≥ 1.5 m with 13 filariae per infected host; <1.2 m with 15 filariae per infected host; and between 1.2 and 1.5 m with 24 filariae per infected host).

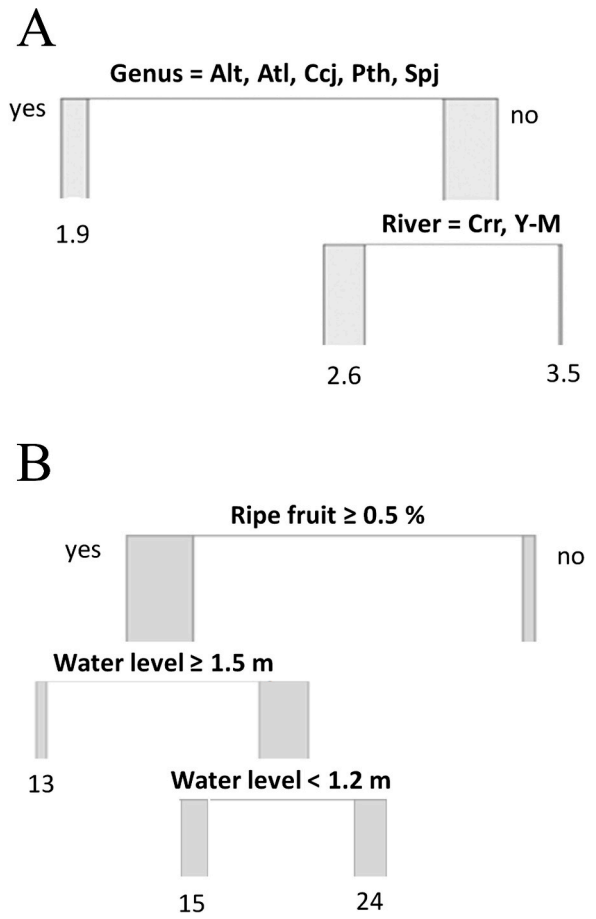


Fig. 1. CART model results of the influence of A) hosts genera (*Alouatta*, Alt; *Ateles*, Atl; *Cacajao*, Ccj; *Cebus; Lagothrix; Phitecia*, Pth; *Saimiri*; and *Sapajus*, Spj; and study areas (Corrientes, Crr; Yavarí-Mirin, Y-M; Pastaza) in the parasitic intensity (number of filariae per infected host), and B) percentage of trees bearing fruits in swamps forests in the parasitic intensity (number of filariae per infected host) in *Lagothrix l. poeppigii* in the Yavari-Mirin River basin (n = 88).

4. Discussion

Parasitological studies in natural environments are essential to the understanding of ecological and biological factors that influence the complexities of transmission and parasite infection in free-living NHP, and the relevance of these to infection risk in humans. However, ecological information on parasites in wild animals is difficult to obtain. As part of a participatory conservation program involving local Amazonian hunters, it was possible to retrieve adult filariae from eight free-living NHP genera. Studies on the prevalence of filarial infection in wild primates are scarce. To our knowledge, only one has been done previously, using molecular techniques to detect filarial infection in African primates (Gaillard et al., 2020), and they found a prevalence of 38%, lower than the 64% we report at our Amazonian site. Our results offer a first point of reference for filarial infections in Neotropical primates, and the participatory methods we used may be a model for the development of further research on filariae indicators in wild mammals in other tropical areas. Our results show differences between NHP genera studied, with higher parasite prevalence and intensity of the infection in *Cebus, Lagothrix* and *Saimiri* compared to *Alouatta* and *Pithecia*.

Recent studies on wild primates indicate that climate and ecological factors have greater effects on parasitism than host physiology (Martínez-Mota et al., 2017). Climatic factors strongly affect vector density, behavior and susceptibility to parasites (Famakinde, 2018). Amazonian rainforests undergo significant seasonal changes during the year, easily measurable through rainfall and river water levels (Endo et al., 2016), that result in seasonal variation in fruit production and maturation (Haugaasen and Peres, 2005) and increases in vector populations during the rainy season, often resulting in increased cases of disease (Kuhn et al., 2005).

Our study showed the influence of environmental variables on the parasitic intensity; lower percentage of trees bearing ripe fruits led to higher numbers of parasites per infected host. During the dry months in the Amazon rainforest, there is a shortage of food for frugivores. This lean period may be temporally alleviated by the fruiting of *Mauritia flexuosa* in swamp-forests (Storti, 1993), the main food consumed by *Cacajao calvus ucayalii* and other primates during these periods (Bowler and Bodmer, 2011), which is seasonal and dependent on edapho-climatic conditions, usually occurring from the end of the rainy season and occasionally extending throughout the dry season. However, the long-term food shortages during the dry period may cause environmental stress in primates, leading to impaired body condition (Stevenson et al., 2000; Dew, 2005) and decreased immune response against parasitic, viral, and bacterial infections (Muehlenbein, 2006; Webster-Marketon and Glaser, 2008). Impairment of immune defenses that modulate the degree of parasite-host balance may be involved in the increased parasite load, but not necessarily in the prevalence of infection.

In our study, the water level is a secondary driver to explain the filariae intensity. When there was no food shortage, intermediate river water levels were related to higher intensity of infection. The rainy season favors mosquito populations, through the increased survival of larvae and life span of adults, increasing the probability of infectious mosquitoes transmitting diseases (Ramasamy and Surrendran, 2012).

Culicoides (Arthropoda: Ceratopogonidae) is the main vector for the

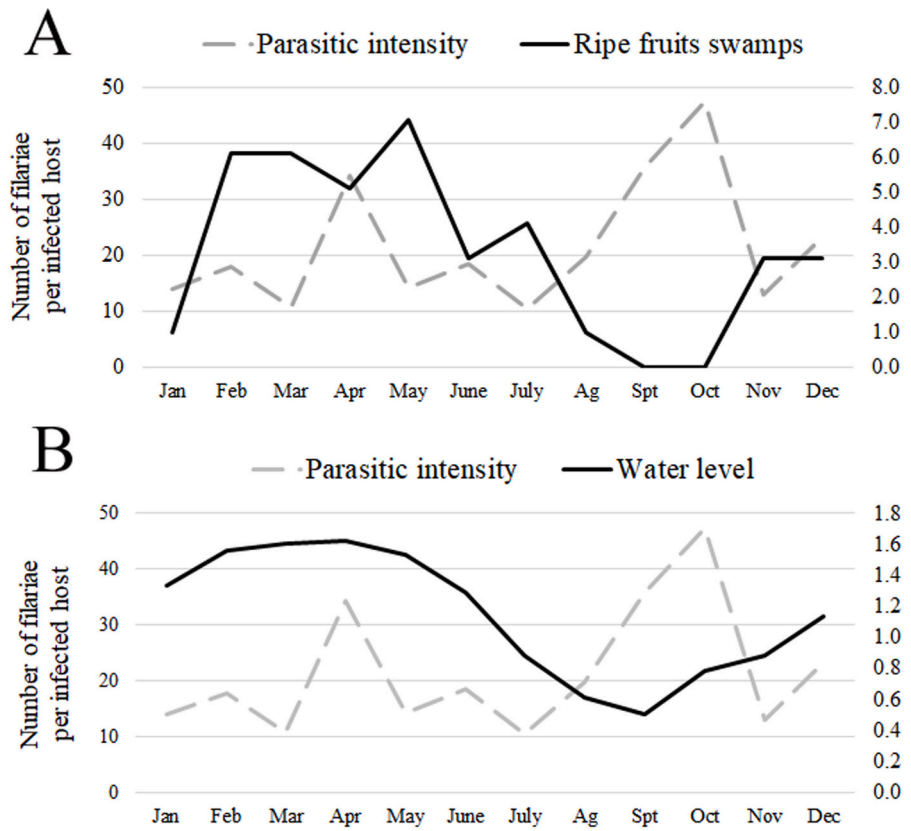


Fig. 2. Trends in river water level, rain days, percentage of trees bearing fruits in swamp forest; and (B) rainfall (dashed line) and parasitic intensity (number of filariae per infected host) in *Lagothrix l. poeppigii* in the Yavari-Mirin River basin ($n = 88$).

microfilariae of the genus *Dipetalonema* in primates (Eberhard et al., 1979; Travi et al., 1985), but Simulids may also act as vectors (Tidwell and Tidwell, 1982). Previous studies showed increasing abundance of *Culicoides* and Simulids during the rainy season in the Amazon (Lacey, 1981; Velasques et al., 2012; Gusmão et al., 2019). However, aalthough mosquitoes require standing water to reproduce, excess rainfall can be disruptive to their reproductive cycle by removing aquatic stages from breeding sites (Benedum et al., 2018), decreasing the incidence of mosquito-borne diseases (Seidahmed and Eltahir, 2016). Vector ecology is key to understanding risk factors associated with infection rate, but we have no supporting information on vector abundance, biting rates and actual infection of the vectors. This lack of information prevents us from explaining the increased parasitic intensity observed during the month of April, which could be related to vector behavior. Further studies are needed to elucidate the relationship between the ecology of vectors and filarial infections.

Beyond climatic factors and fruit shortage, human impacts on habitats have been shown to influence parasite infections in NHP. For instance, logging activities were shown to increase gastrointestinal parasite infections in African primates compared to undisturbed forests (Gillespie et al., 2005). Our results reinforce the importance of palm trees in swamp-forests for conservation, due to their direct contribution to the diet (Fang et al., 2008) and the health status of primate populations.

Despite great efforts to study the ecological and epidemiological mechanisms of diseases, the essential factors determining their transmission cycles are still poorly understood (Weaver and Reisen, 2010). In our study, the prevalence, intensity and abundance of parasites in NHPs were not related to the biological variables studied; probably due to the low sample size in terms of genera. From an ecological point of view, the infection by intestinal nematodes with direct life cycles may regulate the density and distribution of primate populations, by influencing the health and reproductive capacity of hosts (Scott, 1988; Nunn et al., 2003). However, this relationship could be also inverse, in which a higher density of hosts may lead to higher amplification of pathogen transmission (Weaver and Reisen, 2010) and higher concentration and richness of helminths (Arneberg et al., 1998; Morand and Poulin, 1998). Further studies including a large number of species should clarify whether and which of these patterns apply for NHPs in Amazonia.

Studies relating the body mass of hosts and parasitic infection are scarce in wild animals. Larger and heavier wild primates can have more quantities of adult specimen's parasites compared to smaller and lightly hosts (Notarnicola, 2004). Furthermore, susceptibility to mosquito bites probably depends on mosquitoes' preferences for choosing larger hosts because they are more attractive than smaller ones (Takken and Verhulst, 2013), resulting in a positive correlation between host size and parasitic infection (Daviews et al., 1991). However, we found no correlation among those variables in our study area, possibly because primates in natural habitats, opportunities for parasite colonization depend more closely on how hosts are available in a given area than on how large the hosts are (Morand and Poulin, 1998).

In terms of reproductive state, studies on domestic animals show that females in advanced stages of pregnancy stage are more susceptible to parasitic infection than males, due to immune depletion during the gestation period (Jamieson et al., 2006; Henriquez et al., 2010). However, in our study, reproductive state was not significantly correlated with filarial infection, probably due to the small sample size of pregnant females.

5. Conclusion

The dynamics of parasite-host interactions in wild primates may be key to understanding the mechanisms behind filariasis parasitism and transmission in humans living close to tropical forest areas and, consequently, support the development of effective sanitary measures and control of filariasis in this context. In addition, the effects of global

climate change on infectious diseases, especially vector-borne diseases, are uncertain and require ecological information. However, epidemiological data on free-living species are usually scarce, because of the difficulty in obtaining biological and epidemiological samples. This study developed a participatory collection with local subsistence hunters that allowed us to achieve a sufficient sample size to show how climate influence filarial infection in free-living NHP in the rural Amazon. These results may inform predictions on the prevalence and spread of disease in changing climates. We observed a significant difference in parasitic parameters among NHP genera, but the small number of genera studied and the low sample size for some of the genera did not allow observing the effect of biological factors, such as density, group size and body mass, on parasitic parameters. Ecological studies such as the one presented here may improve the understanding of pathogen transmission of neglected diseases in humans that share the same ecosystem, and provide valuable information to study the possible consequences of global warming on the rates of these infections.

Compliance with ethical standards

All applicable institutional and/or national guidelines for the care and use of animals were followed. The research and sample collection protocol were approved by the Peruvian Forestry and Wildlife Service (Ethical Committee for Wildlife Research, N°0350–2012-AG-DGFFS-DGEFFS; N°0249–2013-AG-DGFFS-DGEFFS).

Data availability statement

The data that support the findings of this study are available in the Pangaea repository at 10.1594/PANGAEA.913249 (Conga et al., 2020).

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CRediT authorship contribution statement

David F. Conga: Conceptualization, Writing – original draft. **Hani R. El Bizri:** Formal analysis. **Carlos González Crespo:** Formal analysis, Writing – review & editing. **Luis A. Gomez-Puerta:** Writing – review & editing. **Gabriela M. Ulloa-Urizar:** . **Pedro E. Pérez-Peña:** Data curation, Writing – review & editing. **Mark Bowler:** Writing – review & editing. **Pedro Mayor:** Conceptualization, Visualization, Methodology, Data curation, Writing – original draft.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

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